

## On the relationship of the myotome to the axial skeleton in vertebrate evolution

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*Abstract.*—The traditional belief that vertebrae must alternate in position with the segmented body musculature (myotomes) to allow bending of the axial skeleton is evaluated in terms of the patterns of development and structure of gnathostome vertebrae. The key functional parameter allowing lateral bending of the axial skeleton is the intersegmental position of both the neural and haemal arches, not the centrum. The intersegmental position of both the centrum and arches in tetrapods is the result of a secondary association of the centrum with the primary intersegmental position of the neural and haemal arches. The pattern of vertebral ontogeny and structure in primitive gnathostomes suggests that a causal link between sclerotomic resegmentation during amniote development and the presence of intersegmental vertebrae in the adult is spurious and corroborates the hypothesis that the process of resegmentation evolved as a method of redistributing large volumes of sclerotome cells during development. Patterns of vertebral construction in lower vertebrates are related to fast-start performance and the use of the body as a hybrid oscillator during locomotion.

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### Introduction

Vertebral structure has traditionally been the dominant criterion by which early tetrapods, particularly the Amphibia, have been classified. Vertebral structure in these early forms is highly complex and a correspondingly intricate terminology has developed to describe the anatomy and evolution of the axial skeleton.

Williams (1959) attempted to clarify the terminological confusion by showing that the Gadowian system of vertebral classification, based on the hypothesis that vertebral form was the result of various combinations of embryonic arcualia (Gadow's basidorsals, basiventrals, interdorsals, and interventrals) had no embryological basis. In no vertebrate did Gadow's arcualia appear during ontogeny. Williams' suggestion that this terminology be abandoned in favor of a more embryologically accurate one has been generally accepted and his review has greatly stimulated investigation into patterns of vertebral ontogeny and evolution.

In recent years a number of studies (Andrews and Westoll 1970b; Panchen 1967, 1977; Partridge 1967, 1977) have considered the func-

tional basis for vertebral structure and although some limited success has been achieved (Andrews 1977; Panchen 1977) essentially no testable hypotheses have been generated linking vertebral structure to function, especially in lower vertebrates. In addition, the role of sclerotomic resegmentation in the evolution of tetrapod vertebrae is a matter of some debate (see Schaeffer 1967; Wake 1970; Williams 1959), and yet assumptions underlying hypotheses of sclerotome cell movement during ontogeny frame current conceptions of vertebral homology (see Laerm 1979a).

In spite of several recent reviews of vertebral evolution (Panchen 1977; Schaeffer 1967; Wake 1970) the functional interrelationships of the myotome to the vertebra have not been explicitly treated and the tremendous variation in lower vertebrate vertebral structure has not been used to test hypotheses of the function of sclerotomal resegmentation in tetrapods.

The purpose of this brief review is twofold: (1) To examine the diversity of vertebral structure in lower gnathostomes as a basis for a re-

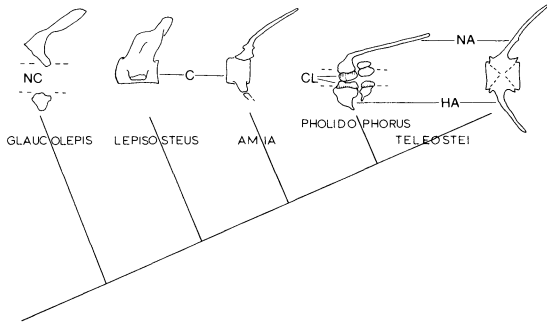


FIGURE 1. Patterns of vertebral structure in some actinopterygian fishes. Anterior is to the left, vertebrae are seen in lateral view, and dashed lines indicate the width of the notochord. Abbreviations: C, centrum; CL, notochordal calcifications; HA, haemal arch and spine; NA, neural arch and spine; NC, notochord. *Glaucolepis* from Nielsen (1942), *Amia* from Schaeffer (1967), and *Pholidophorus* from Patterson (1968).

consideration of the significance of sclerotomal resegmentation and as a guide to reinterpreting the primitive functional association between the myotome and the axial skeleton, and (2) To generate first-order hypotheses relating the occurrence of central ossifications in lower vertebrates to locomotor mode. I will attempt to synthesize some recent studies on fish locomotion with patterns of vertebral structure and indicate how future studies might profitably examine the functional significance of vertebral structure in lower vertebrates.

#### Patterns of Vertebral Structure

I will not exhaustively review vertebral development but only point out key developmental and structural aspects relevant to a consideration of vertebral function.

*Primitive gnathostome vertebrae.*—While the process of sclerotomal resegmentation to form the definitive centrum has been well established in amniotes (Hall 1977; Williams 1959), there is no evidence that resegmentation plays any role in the development of the teleost centrum (Francois 1966; Laerm 1976).

Within the Teleostei, vertebral embryology and form are remarkably consistent. Initially a perichordal tube is formed from sclerotomal cells by the medial migration of these cells to form a continuous layer over the notochord and its sheath, the elastica externa (Farugi 1935;

Laerm 1976). Another membrane layer then differentiates between the externa and the internal notochordal epithelium, the elastica interna. Sclerotomic cells are not arranged metamericly around the notochordal membranes.

The notochordal sheaths then begin to thicken in (ultimately) intervertebral positions causing a depression between the thickened areas. In these depressions centrum development begins. The characteristic amphicoelous shape of the teleost centrum is due to the expansion of the notochordal sheath at the ends of the presumptive centrum and the direct ossification of sclerotomal tissue which essentially molds itself around the biconical expanded sheath.

The centrum always ossifies directly from two main centers (Francois 1967; Laerm 1976; Schaeffer 1967) while the neural and haemal arches are performed in cartilage and subsequently ossify.

A key feature of teleost vertebral development is that the neural and haemal arches need not always be associated with the centrum in a fixed manner. Although in teleosts the arches consistently maintain their association with intersegmental myosepts, they may have a variable relationship to the centra (Farugi 1935). Anteriorly, for example, the neural arch may attach to the anterior of the centrum while in the caudal region it may attach posteriorly. In some forms (*Amia*) the position of the centrum may even be intrasegmental (Schaeffer 1967), the myosepts passing *between* adjacent vertebral centra to attach to the arches. The adult centrum may thus have a variable relationship to the myosept even along the axial skeleton of a single individual.

This pattern is more widespread in non-teleost actinopterygians, the halecomorphs and chondrosteans, where a diplospondylous condition occurs frequently in the caudal region (Nielsen 1942; Patterson 1968) and notochordal calcifications (centra are absent in most groups, Fig. 1) may or may not align with the myosepts.

In primitive ray-finned fishes the notochord is unrestricted and the neural and haemal arches rest on it. In palaeoniscoids (Nielsen 1942) the neural arches were paired and were not fused in the midline dorsally but were probably held together by fibrous connective tissue. Ventrally, the haemal arch elements (basiventrals

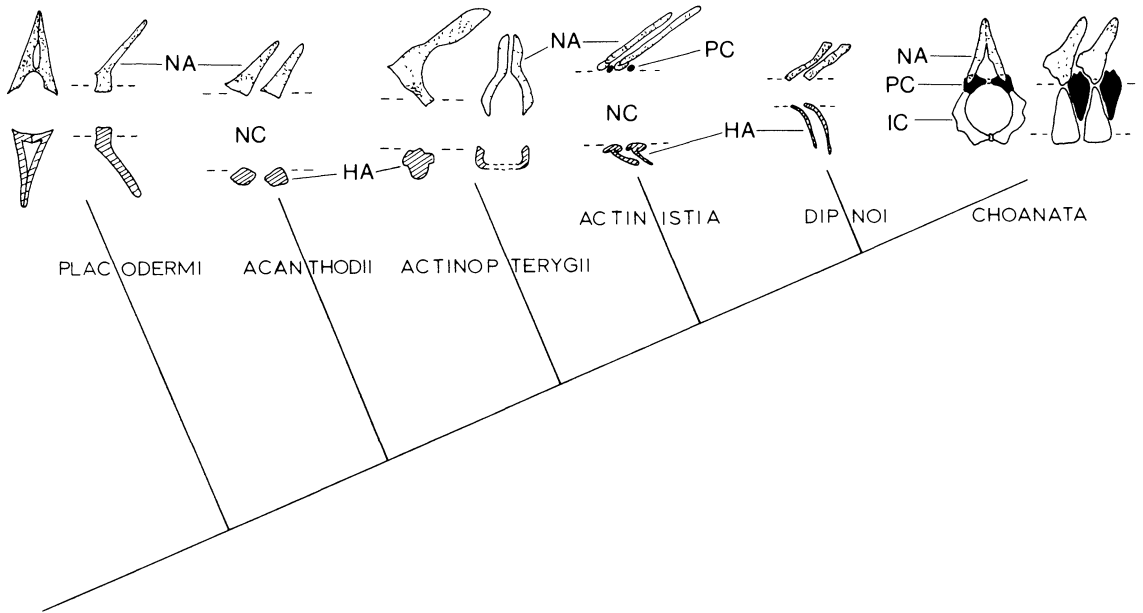


FIGURE 2. Patterns of vertebral structure in primitive members of the major gnathostome groups. Dashed lines indicate the width of the notochord; anterior is to the left. Abbreviations: HA, haemal arch and spine; IC, intercentrum; NA, neural arch; NC, notochord; PC, pleurocentrum. Placodermi (anterior and lateral views) after Miles and Westoll (1968), Acanthodii after Miles (1970), Actinopterygii (anterior and lateral views) after Nielsen (1942), Actinistia after Andrews (1977), Dipnoi after Graham-Smith and Westoll (1937), Choanata (*Osteolepis*) after Andrews and Westoll (1970a).

plus intervertebrals of Nielsen 1942) were paired in some species and fused in others.

In the earliest teleosts (Patterson 1968; Fig. 1) the notochord was essentially unrestricted but there were relatively large paired perichordal calcifications in the notochordal sheaths which may have served to support the arches (Fig. 1: CL). In portions of the caudal region, however, these calcifications occurred in a diplospondylous pattern.

It is clear from this brief review that the primitive condition of the axial skeleton in actinopterygian fishes consists of (1) an unrestricted notochord with small accessory perichordal ossifications and (2) neural and haemal arches which are intersegmental in position *regardless* of the position of the notochordal calcifications or, in teleosts, the centra (Fig. 1). The intersegmental position of the arches is maintained throughout the actinopterygian radiation and allows bending of the axial skeleton by the segmental myotomes during locomotion.

Figure 2 reveals that the features outlined above are actually primitive for all of the major gnathostome groups and thus for gnathostomes as a whole.

In placoderms (Fig. 2) the notochord was large and unrestricted and the neural and haemal arches simply rested on the notochord. Acanthodians had an unrestricted notochord too (Miles 1970) with the dorsal and ventral arches reconstructed as attaching to the external surface of the notochord.

Andrews (1977) has recently redescribed the axial skeleton of *Latimeria* and has demonstrated the presence of neural arch bases, small supportive elements lying on the dorsolateral surface of the greatly expanded notochord (Fig. 2). Small paired pleurocentra are also present posterior to the neural arch bases. Ventrally the small intercentra are serially homologous with the posterior haemal arch bases which support the haemal arches. A thick fibrous connective tissue invests the notochord and holds these small elements tightly to its surface.

In dipnoans the primitive condition is that of other osteichthyan groups—an expanded notochord with the arches attached to the dorsal and ventral notochordal surfaces, presumably by strong connective tissue. Centra have been secondarily acquired in some dipnoans (Jarvik 1952).

The pattern of vertebral structure in non-choanate gnathostomes demonstrates two features of vertebral structure and ontogeny: (1) The neural and haemal arches are always intersegmental and serve as the attachment site for the myosepts. This allows lateral bending of the axial skeleton during locomotion. (2) The process of sclerotomal resegmentation does not occur in non-choanates, although when large ossified vertebral centra do occur they are generally intersegmental (except in the diplospondylous regions).

*Choanate vertebrae.*—Choanate vertebral development and structure have been reviewed by Williams (1959), Panchen (1977), and partially by Wake (1970) and Wake and Lawson (1973), and only a few specific comments will be made here.

There is some controversy over whether the process of sclerotomal resegmentation occurred in the rhipidistian fishes and as to the homologies of the various parts of the rhipidistian vertebral complex. Schaeffer (1967) suggested that resegmentation arose at the rhipidistian–amphibian transition and Laerm (1979a) has claimed that resegmentation did not occur in rhipidistians. Recently Andrews (1977) has homologized the pleurocentra and intercentra of *Eusthenopteron* (Andrews and Westoll 1970a) to those of tetrapods, and Wake and Lawson (1973) stated (*contra* Williams 1959) that the amniote resegmentation pattern has never occurred in salamanders and probably also not in any living or extinct amphibian.

The development of the amniote centrum has been extensively investigated and it is generally accepted that a resegmentation of the sclerotome does occur, the cell rich caudal half of a single segment joining with the cranial half of the next posterior segment to form the embryonic vertebra (Arey 1974; Balinsky 1975; Williams 1959). Verbout (1976), however, has denied that this process occurs in amniotes, but his claim awaits corroboration.

#### Myotome-Vertebral Relationships

*Resegmentation.*—A bias towards the better known pattern of vertebral development in tetrapods and the occurrence of well ossified central elements in amniotes have led to the widespread belief that the presence of sclerotomal

resegmentation as a developmental phenomenon is causally linked to the functional necessity of having myotomes alternate with vertebral elements. This alternation is deemed necessary to allow the myotomal muscle fibers to exert their force across a joint formed between two successive centra and thus cause lateral bending of the axial skeleton. It has not been appreciated that the lack of resegmentation in teleosts and other actinopterygians coupled with the presence of intersegmental vertebral centra fails to corroborate a causal linkage between the occurrence of resegmentation and the intersegmental position of the centrum. This correlation is often either explicitly stated (e.g. Romer and Parsons 1977) or strongly implied (Arey 1974; Hall 1977). It is clear from the above analysis of vertebral structure in non-choanates that there is no need for the *vertebra* to alternate with the myotome. It is, however, necessary that the neural and haemal arches align with the myosepts and in fact this relationship does hold for all gnathostomes. The occurrence of solid intersegmental centra in teleost fishes indicates that resegmentation is not required for alternating myotomes and vertebrae and, conversely, that intersegmental vertebral centra are not necessarily the product of resegmentation (Wake and Lawson 1973), although several workers (notably Williams 1959) have used the intersegmental position of central elements to infer the process of resegmentation.

This analysis tends to corroborate the hypothesis that sclerotomal resegmentation is an adaptation to distributing large volumes of sclerotome cells (Wake and Lawson 1973). Wake and Lawson noted that since the Apoda have the largest mass of sclerotomal tissue in the Lissamphibia and they are the only amphibians known to possess a pattern of vertebral development resembling that in amniotes, therefore the process of resegmentation may have evolved independently in apodans to redistribute sclerotome cells during vertebral ontogeny.

*Functional significance of vertebral structure.*—The functional significance of the various patterns of vertebral structure, especially in osteichthyans, has remained largely obscure. Andrews and Westoll (1970b) made a preliminary attempt to correlate tail shape in rhipidis-

tians with vertebral pattern and found that apsidospondylous vertebrae (characterized by the occurrence of three paired elements: neural arches, intercentra, and pleurocentra) and holospondylous vertebrae (characterized by complete ring-like centra with separate ossified neural arches) both occur in forms with symmetrical or heterocercal tails. No correlations were immediately evident between tail shape and vertebral structure.

I would suggest that a potentially more fruitful approach to the functional significance of vertebral structure may be found by synthesizing recent contributions to fish locomotion, both experimental and theoretical, with studies of body form and the morphology of the axial skeleton in osteichthyans and early tetrapods. The functional significance of different variations in vertebral structure is a second-order question that can only be addressed after first-order functional hypotheses have been generated and tested.

Blight (1977) has, in another context, recently provided a theoretical framework within which to analyze certain aspects of vertebral structure. He has suggested that the vertebrate body be considered as a hybrid oscillator with the main muscle mass anteriorly and little muscle in the tail. The head is in a stiffness dominated mode (reducing head movements during locomotion) while the tail is in a resistance dominated mode. The stiffness of the tail is under muscular control and is increased during high accelerations.

This model provides an explanation for one of the most common regional changes in the vertebral column—from a monospondylous condition in the thoracic region to diplospondyly in caudal vertebrae. Diplospondylous vertebrae allow a much greater degree of control over locomotor pattern since the frequency of the tail as an oscillator can be controlled both within a wider range and to a finer degree than with a monospondylous condition.

The large unrestricted notochord in certain rhipidistians (e.g. *Eusthenopteron*) and primitive members of all the major osteichthyan groups imposed considerable constraints on the locomotory pattern since notochordal diameter, a fixed parameter, cannot be changed rapidly to generate a change in stiffness; changes in tail stiffness are necessary during periods of rapid

acceleration. The development of relatively more massive vertebrae (including intercentra, pleurocentra, and expanded neural and haemal arches) in rhipidistians almost certainly allowed a greater control over body and tail flexibility, and this greater range of body oscillator frequencies may have been an extremely important factor in allowing the transition to a terrestrial locomotor mode.

The correlation between body and tail oscillator frequencies and general patterns of vertebral structure receives further support from recent analyses of fast-start performance in teleost fishes (Webb 1976, 1977, 1978). Webb (1978) and Weihs (1973) have concluded that fast-start performance, the rapid acceleration from an initial rest position, is maximized by two parameters—lateral body and fin area and the muscle mass acting to generate thrust. For improved fast-start performance, maximum lateral body profile should be located far posterior to the center of mass of the fish. An hypothesis using fast-start performance and the hybrid oscillator as a model with which to predict the distribution of certain patterns of vertebral structure would suggest that more massively ossified centra will tend to occur in those groups which show improved fast-start performance and thus those with greater fin area posteriorly and/or greater masses of body musculature acting on the tail oscillator. In three groups, this holds remarkably well.

The palaeoniscoid fishes probably had very poor fast-start performance. Possessing only a single dorsal fin, the point of greatest body depth was located approximately over the center of mass. This, however, is not true for teleost fishes, *Amia* and *Lepisosteus* which possess both well ossified centra and good fast-start performance (Fig. 1).

Interestingly, the dipnoans with ossified centra (e.g. *Rhynchodipterus*) have considerable fin area located far posterior to the estimated center of mass, much more so than in dipnoans with unrestricted notochords.

The rhipidistians also have posteriorly located fins, both dorsal fins attaching to the posterior half of the body. This probably reflects improved fast-start performance and correlates with increased vertebral ossification surrounding and constricting the notochord.

Laerm (1979b) has suggested that the intercalaries (notochordal calcifications) in many primitive actinopterygians may have functioned as "space-filling axial compression members between the arch bases." Although the distribution of the notochordal elements in chondrosteian taxa remains to be correlated with locomotor performance as suggested above, the key role of intercalaries (as well as other central elements) is more likely a dual one: they serve as axial compression members *while permitting bending* of the the tail and body. (See Wainwright et al. 1976 for a discussion of the design of structures subject to both compressive loads and bending moments.)

These general first-order correlations between vertebral structure and locomotor pattern are necessarily imprecise since they reflect both our lack of knowledge regarding the structure of many fossil forms and the relatively incomplete nature of functional studies on the locomotion of fishes. These correlations do nonetheless indicate that this approach to the relationship between form and function of the axial skeleton may provide the first testable hypotheses relating function to vertebral structure in lower vertebrates.

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